



INFLUENCE OF GONADAL MATURATION ON GLYCOSAMINOGLYCAN LEVEL IN *Prochilodus brevis* SKELETAL MUSCLE

INFLUÊNCIA DA MATURAÇÃO GONADAL SOBRE O NÍVEL DE GLICOSAMINOGLICANOS NO MÚSCULO ESQUELÉTICO DE *Prochilodus brevis*

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Resumo

Desconhecido é o papel de glicosaminoglicanos (GAGs) na maturidade sexual de *Prochilodus brevis*. Neste estudo a influência da maturação gonadal foi avaliada no músculo esquelético de *P. brevis* sobre o nível de GAGs. Foram selecionadas e examinadas, de machos-M e fêmeas-F (167,30 ± 6,66-M / 209,50 ± 39,30 g-F, n = 4), gônadas por macroscopia e índice gonadossomático (IGS) antecedendo à filetagem para determinação (%; m m⁻¹) de músculo fresco / desidratado, conteúdo de água (CA) por diferença de massa após estufa e, comparando-se rendimento, metacromasia com corante catiônico e espectroscopia de infravermelho estruturalmente, a extração com papaína de GAGs intramusculares. Os resultados mostraram que refletindo (%; p < 0,05) do estágio gonadal no peso (2,24 ± 0,59-M vs 15,42 ± 3,48-F) e IGS (2,30 ± 0,62-M vs 18,81 ± 4,60-F) não alteraram (p > 0,05) massa de filé de peixe (22,69 ± 1,24-M vs 20,75 ± 3,51%-F, fresco / 5,17 ± 0,21-M vs 5,72 ± 0,46%-F, desidratado) e CA (77,49 ± 0,72-M vs 69,19 ± 7,49%-F), porém de GAGs diferiram rendimento (0,09 ± 0,01-M vs 0,02 ± 0,00%-F, p < 0,05), caráter aniônico e composição estrutural em dermatana e/ou queratana entre sexos. O estudo sugeriu que os GAGs do músculo, como fontes bioenergéticas, podem contribuir na reprodução de *P. brevis*.

Palavras-chaves: Peixe reofilico, Maturidade sexual, Polímeros sulfatados, Demanda energética, Reprodução.

Abstract

The role of glycosaminoglycans (GAGs) on the sexual maturity of *Prochilodus brevis* is unknown. In this study evaluated the influence of gonadal maturation on GAGs level in *P. brevis* skeletal muscle. Male-M and female-F (167.30 ± 6.66 -M / 209.50 ± 39.30 g-F, $n = 4$) gonads were selected and examined by macroscopy and gonadosomatic index (GSI) prior to filleting for determination (% w w⁻¹) of *in natura* / dehydrated muscle, water content (WC) after oven per mass difference and intramuscular GAGs extraction with papain comparing yield, metachromasy with cationic dye and structurally by infrared spectroscopy. The results showed that the gonadal stage reflecting (% $p < 0.05$) in weight (2.24 ± 0.59 -M vs 15.42 ± 3.48 -F) and GSI (2.30 ± 0.62 -M vs 18.81 ± 4.60 -F) did not change ($p > 0.05$) the mass of fish fillet (22.69 ± 1.24 -M vs 20.75 ± 3.51 %-F, *in natura* / 5.17 ± 0.21 -M vs 5.72 ± 0.46 %-F, dehydrated) and WC (77.49 ± 0.72 -M vs 69.19 ± 7.49 %-F), but yield (0.09 ± 0.01 -M vs 0.02 ± 0.00 %-F, $p < 0.05$), anionic character and structural composition of GAGs differed in dermatan and/or keratan between sexes. The study suggested that the muscle' GAGs may contribute as bioenergetic sources in reproduction of *P. brevis*.

Keywords: Rheophilic fish, Sexual maturity, Sulfated polymers, Energetic demand, Reproduction.



Introduction

Fish have various adaptive strategies (e.g., parthenogenesis, bisexuality, and hermaphroditism) (Moreira et al., 2001) depending on the climatic signals (e.g., temperature, season and rainfall pattern) (Baldisserotto, 2002) conditioning the species with changes or not in body standard (Araújo et al., 2018; Santos et al., 2001; Rodrigues et al., 2026). *Prochilodus* Agassiz (1829) have been marketed (*P. lineatus* Valenciennes, 1837 and *P. scrofa* Steindachner, 1881 - Moreira et al. (2001); *P. nigricans* Agassiz, 1829 - Souza and Inhamuns (2011)) or, until, considered to polyculture (*P. lineatus* - Borba et al. (2026)). Common curimatã *P. brevis* Steindachner (1875) (Bomfim et al., 2015; Leite et al., 2018; Salmito-Vanderley et al., 2023; Santos et al., 2026) occurs as a migratory species in hydrographic basins of northeast Brazil (Gurgel et al., 2012) or when introduced into the private reservoirs (Nascimento et al., 2012; Salmito-Vanderley et al., 2023; Santos et al., 2026), but for evaluating of the potential in aquaculture, its reproduction in captivity is conditioned by human intervention (Leite et al., 2018; Vieira et al., 2024).

P. brevis (Prochilodontidae; Characiformes) is, notably, a rheophylic species considered as a promising regional candidate for fish farming, since it has favorable indicators for its reproductive management, nutrition (Gurgel et al., 2012; Bomfim et al., 2015), fingerling production (Bomfim et al., 2015), seminal preservation (Nascimento et al., 2021; Salmito-Vanderley et al., 2023) and technological perspectives (Santiago et al., 2024; Fernandes et al., 2025; Santos et al., 2026). Its roe is also popularly consumed by humans revealing economic values in Brazil (Bomfim et al., 2015).

Teleost fish have biological variations or not associated with the ontogenetic period (Soares et al., 2021). Sales & Sales (1990) analyzed edible (muscle + bones) samples of ten species (*Tilapia melanopleura* Dumeril, *Cichla acellaria* Schneider, *Triportheus angulatus angulatus* Spix, *P. cearensis* - currently known as *P. brevis*, *Plagioscion squamosissimus* Heckel, *Hoplias malabaricus* Bloch, *Leporinus friderici* Bloch, *Leporinus* sp., *Trachycorystes* sp. and *Curimatã* sp.) caught and found that their centesimal composition varied with the somatic factors (age, gender, nutrition, time of the year and site of capture), especially at the high protein level, a good nutritional attribute. Fish-muscle proximate composition would reflect the animal demand not only from the natural environment (Araújo et al., 2018; Cosme et al., 2022), but also from confined one (Moreira et al., 2001). Circular economy-based principles for *P. brevis* have created novel biological bases for the valorization of aquaculture discards within ichthyoglycobiology (Fernandes et al., 2025).

Within animal-derived biomaterials have glycosaminoglycans (GAGs), a family of complex polysaccharides found in vertebrate and invertebrate (Pomin & Mourão, 2008; Badri et al., 2018). GAGs play functions since innate defense in osmoregulation (Rodrigues et al., 2025) to animal speciation (Pomin & Mourão, 2008). GAGs-mediated physiological processes interact with proteins (e.g., growth factors) of cell surface of numerous tissues, displaying signaling pathways and, possibly, as disease biomarkers (Ricard-Blum et al., 2024). The quality standard of GAGs is based on



animal source (Pomin & Mourão, 2008; Badri et al., 2018; Fernandes et al., 2025), type of first-matter (Fernandes et al., 2025) and method employed (Badri et al., 2018; Balbinot-Alfaro et al., 2021), although some chemically developed or by heterologous production (Badri et al., 2018) implicated in metabolism of cancer and inflammation (Ricard-Blum et al., 2024). They have unbranches chains, constutred by repetitive disaccharide units of a hexosamine (D-glucosamine or D-galactosamine) and uronic acid (D-glucuronic or L-iduronic) or galactose units, being linear and highly charged, but varying in sulfation pattern, glycosidic linkage and specific sugar sequence. As more known have heparin (HEP, highly charged), chondroitin sulfate (CS), dermatan sulfate (DS), hyaluronic acid (HA, nonsulfated), keratan sulfate (KS) and heparan sulfate (HS) (Badri et al., 2018; Balbinot-Alfaro et al., 2021) participating of the extracellular matrix organization (Ricard-Blum et al., 2024) and animal development (Pfeiler et al., 1998; Zhang et a., 2009). Terrestrial source-derived GAGs are of highly viral risk (Badri et al., 2018; Balbinot-Alfaro et al., 2021), therefore, those from aquatic sources arise as more safe alternatives (Pomin & Mourão, 2008).

As ectothermic organisms (Moreira et al., 2001; Rodrigues et al., 2026), fish skeletal muscle has different composition and structure that than found in terrestrial mammals, as a result of the environmental differences in which the animals are found (Hannesson et al., 2007). Structural differences in the overall organization of muscle fiber and connective tissue became challenger in the recovery of polymers, and their association with the animal physiological responses may provide useful data regarding structure-function, within food sciences field (Ogawa & Maia, 1999). Tingbo et al. (2005) examined in muscle tissue for GAGs, extracted from spotted wolffish, *Anarhichas minor* (a non-gaping species), and from Atlantic cod, *Gadus morhua* (a gaping species), and discovered that the sulfate anionic composition differed not only between both fish species, but also in type of GAG present in the intramuscular matrix. Even for GAGs extracted from bovine (Norwegian red) and Atlantic cod (*G. morhua*) skeletal muscle, Hannesson et al. (2007) identified, by biochemical and microscopy techniques, the expression of CS and KS varying between both animals, possibly implying them in their functional requirements as to the fibrous appearance and texture of muscle. Other aquatic animals muscle GAGs-related data were already reported for specimens of cuttlefish (*Sepia officinallis* - Jridi et al., 2019), salmons (*Salmo salar* - Jacobsen et al., 2019), flounders (Wang et al., 2024) and shrimps (*Litopenaeus vannamei* - Cordeiro et al., 2026) on their compositional knowledge of the extracellular matrix and related factors. *P. brevis* has no apparent sexual dimorphism and the sacrifice of the fish proves to be decisive for sexing (Gurgel et al., 2012; Nascimento et al., 2012; Bomfim et al., 2015; Santos et al., 2026), however, its muscle GAGs composition remain unexplored so far, since the reproductive season alters in the animals the parameters of semen (Leite et al., 2018), but not anatomically, the specimens (Santos et al., 2026).

The aim of this study was to examine the influence of gonadal maturation, determined by weight and gonadosomatic index, on the GAGs level in *P. brevis*



muscle tissue removed from bony skeleton by a filleting manual operation of males and females collected in reproductive season and then experimentally adapted in captivity; and, thereafter, by comparing the charge density and the structural composition of sulfated GAGs by classical biochemical and structural approaches, aiming thus to contribute with novel indicators related to physiological status associated with the conservation and ecological preservation, as well as technological sustainability inside the sexually matured gender presenting the total spawning as reproductive strategy.

Material and Methods

Matured specimens of *P. brevis* gender

Originally, fish were collected from a reservoir in the municipality of Canindé-CE, Brazil, and then adapted, in laboratory conditions, for about two months in a permanent system of recirculation tank (7,000 L). Fish were previously analyzed by ultrasonographically and morphologically for predicting the sex of the animals (Salmito-Vanderley et al., 2023).

Adult individuals of both males and females (n = 4, for each gender), under evident gonadal maturation stages, were initially selected for sampling from a previous profile of body standard recently analyzed by Santos et al. (2026) for this captive species. Further, fish were submitted to persuasive stunning and, immediately, transported in ice (1:1 k biomass: ice ratio) at sialed isothermal boxes by the Fish Reproduction Biotechnology Laboratory (State University of Ceará, SUC, in Fortaleza city) to the Marine Biochemical (MarBio) laboratory located at Aquaculture Biotechnology Center, Department of Fisheries Engineering, Federal University of Ceará (FUC), where the Brazilian bocachico was subjected to biometric (cm) and body (kg or g) sampling (Table 1) before the yield and biochemical analyses from the fish muscle. Fish were authorized through our registration with SISGEN-AA4816B (National System for the Management of Genetic Heritage and Associated Traditional Knowledge) and approved by the Ethical Committee of the SUC (protocol no. 6699198/2017).

Table 1. Water, body weight and biometric parameters of captive *P. brevis*.

Parameters*	Males	Females
n (individuals)	4	4
Total biomass (kg)	669.01	838.16
Length (cm)	23.25 ± 0.40	24.28 ± 1.33
Weight (g)	167.3 ± 6.66	209.5 ± 39.30
Height (cm)	5.42 ± 0.14	5.50 ± 0.30
Furcal length (cm)	20.85 ± 0.59	20.63 ± 1.14
Standard length (cm)	18.70 ± 0.64	19.63 ± 1.20
Trunk length (cm)	10.38 ± 0.68	11.43 ± 0.31
Head length (cm)	4.55 ± 0.16	4.47 ± 0.34
Stocking density (fish L ⁻¹)	0.20	
Feed rate (%)	1.00	
Temperature (°C)	26.5-29.5	



Dissolved oxygen (mg L ⁻¹)	7.00
pH	7.00
Total ammonia (mg L ⁻¹)	0.25
Cultivation system	rectangular fiber tank with aeration system

*water parameters measured by portable equipment; and body weight and biometric data of relatively randomized animals determined by balance (g) and rudimentary ichthyometer (cm), respectively, previously obtained (Salmito-Vanderley et al., 2023; Santos et al., 2026).

Experimental design

It was adopted an entirely aligned protocol using an equal number of relatively homogeneous animals in body standard by gender (males vs. females, n = 4 per group) (Table 1) (Leite et al., 2018; Santos et al., 2026). Of silvery coloration, fish were sexed by macroscopy and gonadosomatic index according to the both physiological status of the gonads allocated in the abdominal cavity, of which they were extracted by longitudinal incision and then the weight (g), in grams, determined for each specimen (Nascimento et al., 2012; Bomfim et al., 2015). To assess whether there was any influence of the gonadal maturation stage, the relative level of sulfated GAGs present in *P. brevis* muscle tissue was quantitatively and biochemically sampled between both sexes inside the reproductive season. Before these analyses, a technique of headless filleting was used for manually removing of the fresh edible mass devoid of skin from the fish bony skeleton, as previously applied to this species, when eviscerated (Figure 1) (Santos et al., 2026).

After that, both matured *P. brevis*-derived skinless fillets were separately quantified and dehydrated for the water content determination and, thereafter, subjected to sequential GAGs extraction, in an attempt to evaluate the efficacy and the overall amount recovered from the edible extracellular matrix comparing per analyzed animal group. For examining, subsequently, as possible molecular bioindicators related to physiological status of the animals, in its reproductive period, the metachromasy and infrared spectroscopy assays for partial anionic character and structural featuring were also employed as combined (biochemical / structural) tools inferring molecular properties for animal tissues' sulfated GAGs (Pfeiler et al., 1998; Jridi et al., 2019; Fernandes et al., 2025; Cordeiro et al., 2026); besides, how by which they could also be technological implications in the edible mass composition of *P. brevis* categorized by sexes, being such experimental approaches sequentially illustrated in figure 1 and then described below.



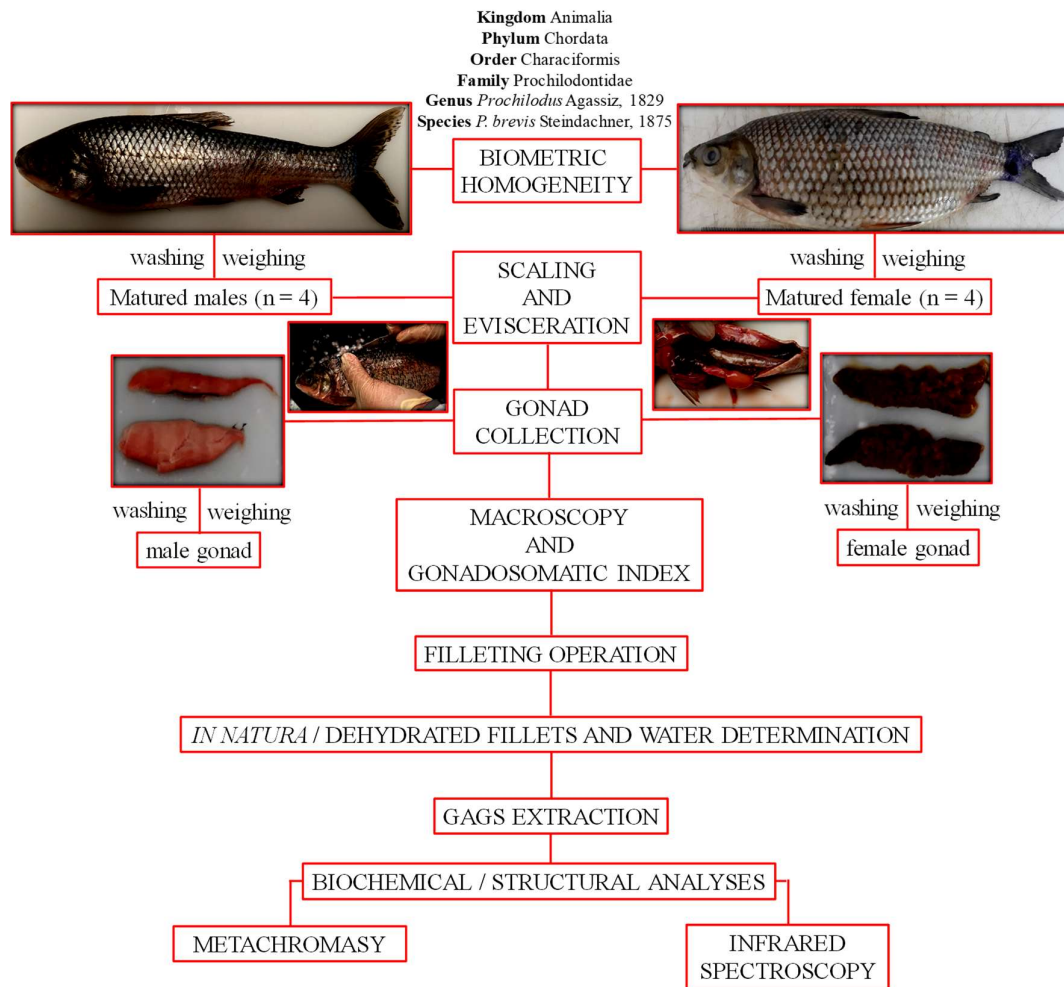


Figure 1. Matured *P. brevis* experimental processing-descriptive scheme from animal' sexing to partial characterization of its skinless fillet-extracted GAGs.

Gonadal analysis

For the gonadal tissue extracted from the abdominal cavity and macroscopically analyzed the weight (g) was obtained, in grams, when separately determined by sexes. Further, it was estimated the current stage of fish gonadal maturation that was achieved according to the average data of the gonadosomatic index (GSI) commonly applied for *P. brevis* (Gurgel et al., 2012; Nascimento et al., 2012; Bomfim et al., 2015; Salmito-Vanderley et al., 2023; Santos et al., 2026) as another biological indicator, according to the Equation 1:

$$\text{GSI} = \text{gonad weight (g)} / \text{fish weight (g)} \times 100 \text{ (Eq. 1)}$$

Filleting operation and determination of fish edible mass

Measured and washed individuals (Table 1) were then submitted to a procedure of filleting by a single operator using previously eviscerated animals divided per gender (Figure 1), whose method initially consisted by fish head separation by straight cut from the animal' trunk (Araújo et al., 2018; Cosme et al., 2022), followed by removing of the skin tissue through of an incision with a knife in the dorsal region extending along the peripheral cut area of the fish considering

from the vertebral structure to the end of the ribs (Moreira et al., 2001; Rodrigues et al., 2026). So, the skin waste was separated from the skeletal muscle manually or, when necessary, by clamp (Figure 2) (Rodrigues et al., 2026) as also previously described by Santos et al. (2026) investigating this same species of fusiform body shape, but no showing sexual dimorphism (Nascimento et al., 2012).

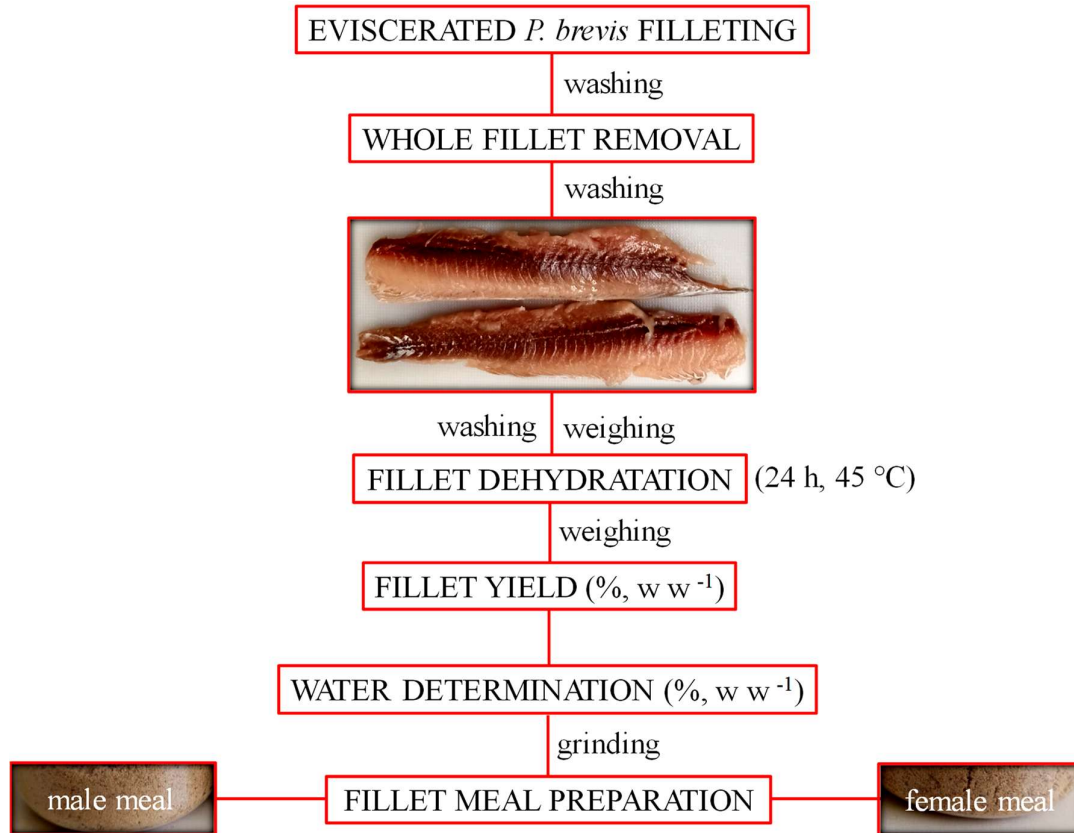


Figure 2. Matured *P. brevis* filleting operation and steps for obtaining of skinless fillet and its meal preparation from both gender.

After filleting, the *in natura* edible part was quantified (% w w⁻¹) from the weight of fish (Equation 2) as already demonstrated for *P. brevis* (Santos et al., 2026) and other freshwater teleosts (Santos et al., 2001; Araújo et al., 2018; Cosme et al., 2022; Rodrigues et al., 2026). Next, the *P. brevis* muscle samples were reduced their intramuscular water composition by mean of dehydration at 45 °C for 24 h using an oven drying with activated air circulation as applied for other aquatic animal' tissues before the GAGs extraction procedure, and then it was also calculated the relative yield (% w w⁻¹) based on initial first-matter (Equation 2) (Fernandes et al., 2025; Rodrigues et al., 2025; Cordeiro et al., 2026). So, both edible portions were mechanically triturated (25-28 °C), with three rotation cycles of 1 min each, to obtain a fine powder, being thereafter, the produced material stored in plastic recipient, separately, until GAGs extraction (Cordeiro et al., 2026).

$$\text{Fillet yield (\%, n = 4 per gender): } \text{fish fillet fish weight}^{-1} \times 100 \text{ (Eq. 2)}$$

Regarding skinless fillet water content, *P. brevis* material samples were weighted (fresh vs. dehydrated) to determine by difference their relative masses

after 24 h dehydration period, as based on Rodrigues et al. (2025) applying for fish skin, following the Equation 3:

Water content ($n = 4$): fresh fillet dehydrated fillet⁻¹ × 100, or water loss -1 (Eq. 3)

Fillet GAGs extraction

Dehydrated skinless fillets of captive *P. brevis* with the same body mass between the sexes (Table 1), which were transformed into a fine powder (Figure 2), they were used for extracting of crude GAGs from powdered muscle samples (about 10 g tissue) by proteolytic digestion with 10% crude papain (w w⁻¹) using a thermostatic bath (60 °C), in a buffer-system made of 100 mM sodium acetate buffer (pH 5.0) containing both 5 mM EDTA and 5 mM cysteine. The extraction period was developed by overnight (Fernandes et al., 2025; Rodrigues et al., 2025) as also adapted with the study of Cordeiro et al. (2026) for pre-processed shrimp muscle (Figure 3).

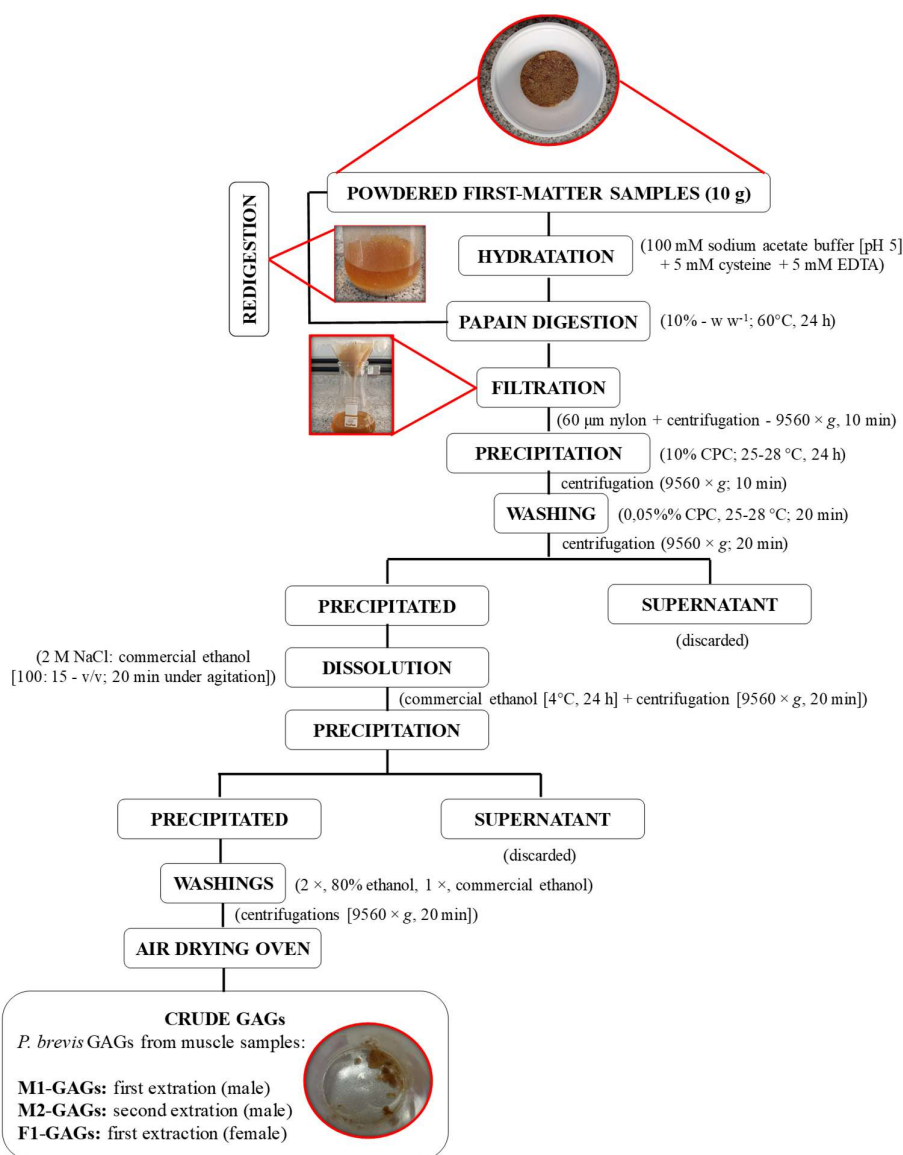


Figure 3. Powdered fillet tissue of matured *P. brevis* fish submitted sequentially to protease incubation for intramuscular GAGs extraction.

Fish material was recovered after 24 h extraction period, being the mixture continually filtered using a 60 µm nylon net, whose supernatant was saved and then centrifugated (9.560 × g for 20 min). Further, GAGs that were present in filtered medium were concentrated with 5 mL of 10% cetylpyridinium chloride (CPC) solution at room temperature (25-28°C) for 24 h precipitation period. After that, the mixture centrifuged at 9.560 × g for 20 min resulted in a pellet that contained the GAGs, which were then washed with 100 mL of 0.05% CPC solution, dissolved (under mechanical stirring for 20 min) in 100 mL of a 2 M NaCl: 92.8% ethanol (100:15 ratio, v:v) solution, followed by other step of precipitation (24 h, 4°C) by adding of 100 mL of 92.8% ice-cold commercial ethanol. The recovered product was centrifugated (9.560 × g for 20 min) and washed with 100 mL of 92.8% commercial ethanol. After each centrifugation (9.560 × g for 20 min) among the mentioned steps, the partially purified material was dried using an oven with air circulation (60°C, 6 h) to obtain the crude LvGAGs extract. To optimizing the total yield for GAGs, the residual mass was redigested applying the same conditions as for those obtained from seaweeds (Pomin & Mourão, 2008), whose products received the following nomenclatures: M1-GAGs and M2-GAGs for *P. brevis* male fillet GAGs derived from first and second extractions, respectively: and F1-GAGs for those from first extraction of female fillet. The total extraction yield was calculated as the percentage (w w⁻¹ %, n = 3) based on both dehydrated first-matters (g) as also estimated for those of shrimp muscle by Cordeiro et al. (2026), according to the Equation 4 below:

$$P. brevis \text{ fillet GAGs yield (\%, w w}^{-1}\text{): fish muscle material weight}^{-1} \times 100 \text{ (Eq. 4)}$$

Metachromatic evaluation

For this assay, *P. brevis* GAGs from fillet samples (both gender) were indirectly checked for metachromasy from solutions of crude extracts previously prepared in distilled water and aliquots varying from 9 to 27 µg (w v⁻¹) were progressively tested with the 1,9 dimethylmetilene blue (DMB) cationic dye, traditionally employed as an indirect indicator for sulfated materials by colorimetric reaction reflecting the complex formed (Farndale et al., 1976). The *in vitro* assay of metachromatic reaction was performed following other related studies (Fernandes et al., 2025; Rodrigues et al., 2025; Cordeiro et al., 2026) for animal' tissues-derived GAGs, in triplicate, using glass tubes (24-28°C), being the violet property as product of reaction visualized to be specific for sulfated GAGs. For digital data, the results were also recorded by photographic images from a portable device of 50 megapiexels resolution.

Fourier Transform Infrared (FT-IR) spectroscopy

The structural composition of *P. brevis* GAGs from fillet samples (both gender) were recorded by a FT-IR spectrometer of IRPrestige-21 Shimadzu, Japan. For this, test sample was previously weighed (~10 mg) for pressing in potassium bromide (KBr) (Fernandes et al. 2025; Rodrigues et al., 2025; Cordeiro et al., 2026). The measurements were generated from pellets at a resolution of 4 cm⁻¹, with 64 scans min⁻¹ at wavenumber 500-4000 cm⁻¹. The spectral values and the graphicals



were assigned and represented using the Origin software version 8.0 as the Statistical Analysis Software (USA).

Statistical treatment

This study followed a completely randomized experimental design and all the data were expressed as mean $\pm$ standard deviation. Fillet, water rate and GSI profiles were analyzed by Student' *T*-test, with $p < 0.05$ as significant. For GAGs yield comparison between both gender, statistical performance was conducted by one-way ANOVA, followed by Tukey' test, applying $p < 0.05$ as significant. The statistical analyses were done using the GraphPad Prism® version 5.01 for Windows (GraphPad Software, 1992-2007, San Diego, CA; www.graphpad.com).

Results and discussion

Since the 90's, *P. brevis* has been focused on its reproductive biology (Gurgel et al., 2012; Nascimento et al., 2012; Bomfim et al., 2015) with involved factors (Sales & Sales, 1990; Leite et al., 2018) and how to make it feasible in captivity for the production and conservation of this species (Salmito-Vanderley et al., 2023; Leite et al., 2018) with industrial perspectives (Santiago et al., 2024; Fernandes et al., 2025; Santos et al., 2026). We now report the influence of a well-defined stage of gonadal development previously analyzed by macroscopy and GSI on the GAGs level in *P. brevis* skeletal muscle for matured males and females with relative homogeneity in terms of size and weight (Table 1), as pre-analyzed somatic factors that determine its reproductive viability and body standard unrelated to sexual dimorphism as evidenced in the wild (Gurgel et al., 2012; Nascimento et al., 2012; Bomfim et al., 2015) and culture (Salmito-Vanderley et al., 2023; Santos et al., 2026) environments, aiming here other biochemical aspects, in part, involved in its reproductive cycle of total spawning (Leite et al., 2018; Vieira et al., 2024).

Gonadal analysis

Both gender of captive *P. brevis* were initially chosen under rigorous qualitative aspects of their gonads extracted from the abdominal cavity by invasive method from longitudinally eviscerated individuals (Figure 1) (Nascimento et al., 2012; Bomfim et al., 2015; Santos et al., 2026). Then, they were macroscopically inspected for evaluating of GSI within universe of 15 specimens (Santos et al., 2026), being the anatomy of fish also selected in an equal number of four sexually viable individuals for sampling of biological data comparing some authors (Table 2).

Table 2. Gonadal parameters of captive *P. brevis* in comparison with other authors.

Gonad	Male (n)	Female (n)	Origin (Brazil)	Reference
total biomass (g)	15.40 (4)	130.23 (4)	reservoir (Canindé-CE)	this study
	35.15 (10)	134.84 (5)	reservoir (Canindé-CE)	Santos et al. (2026)
weight (g)	3.85 $\pm$ 1.08	32.74 $\pm$ 9.64	reservoir	this study



	(4) ^a	(4) ^b	(Canindé-CE)	
	2.09 (13)	16.40 (3)	Piranhas-Assu basin (RN, PB)	Gurgel et al. (2012)
			fish farming	
	0.90 ± 0.47	3.25 ± 2.05	(137 specimens)	Bomfim et al. (2015)
	3.32 ± 1.37	25.51 ± 21.11	reservoir	Santos et al. (2026)
	(10)	(5)	(Canindé-CE)	
weight (%)	2.24 ± 0.59	15.42 ± 3.48	fish farming	this study
	(4) ^a	(4) ^b	(8 specimens)	
	2.20 ± 0.90	16.74 ± 8.44	reservoir	Santos et al. (2026)
	(10)	(5)	(Canindé-CE)	
gonad:body ratio (g, %)	1.01 ± 0.00 ^a ,	0.15 ± 0.03 ^b ,	reservoir	this study
	2.30 (4)	15.53 (4)	(Canindé-CE)	
GSI (%)	2.30 ± 0.62	18.81 ± 4.60	reservoir	this study
	(4) ^a	(4) ^b	(Canindé-CE)	
	4.15 ± 4.08 (maximum in period) (-)		Piranhas-Assu basin (RN, PB)	Gurgel et al. (2012)
	6.00 (-)	20.08 (-)	Marechal Dutra reservoir (RN)	Nascimento et al. (2012)
			fish farming	
	3.38 ± 1.52	14.12 ± 5.59	(137 specimens)	Bomfim et al. (2015)

Different letters indicate statistical significance between sexes at level of 5% (Student' T-test, $p < 0.05$, $n = 4$ or (-) not informed).

As can be seen (Table 2), there was a direct connection among the organ-related weight indexes and the GSI as indicator in the functional stage of the gonads (males and females) inside the reproductive phase of this species (Gurgel et al., 2012; Nascimento et al., 2012; Bomfim et al., 2015; Santos et al., 2026). Obviously, this scenario corresponded for a very reduced sample size, but it concisely reflected the chances in anatomy and gonadal structure unrelated to fusiform body standard of *P. brevis* as also already demonstrated (Santos et al., 2026), since macroscopically, the female gonad occupies a greater volume of the abdominal cavity with a greyish-green structure and well-vascularized, whereas the testicles in males near the spermiation (pink or milky white color) (Bomfim et al., 2015; Santos et al., 2026) as examined in figure 1. On these stages, Leite et al. (2018) observed that the sazonality influence in physical, kinetic, morphological and biochemical characteristics of semen of *P. brevis* in its reproductive period, and also yet in the quality of plasma.

As the environmental factors modulate the physiological responses of aquatic organisms and determine their success in terms of the periodicity and extension or not of reproductive cycles (Baldiasserotto, 2002; Pomin & Mourão, 2008) and, consequently (Moreira et al., 2001), what economic effects



environmental variations would have on the aquaculture sector? To explore this question, we analyzed the impact of the maturation of *P. brevis* on the skinless fillet yield and the relative rate of water between the sexes considering technological utilizing (Ogawa & Maia, 1999) based on other producer species (Santos et al., 2001; Souza & Inhamuns, 2011; Araújo et al., 2018; Borba et al., 2026), since the body / weight values of analyzed individuals (Table 1) are within the reproductive cycle of *P. brevis* (Nascimento et al., 2012; Bomfim et al., 2015).

Relative yield of fillet and its water content

On a mass-to-mass basis, the figure 4 illustrates the relative yield in terms of fillet (*in natura* vs. dehydrated) production and the respective percentage of water obtained per difference between both *P. brevis*-derived edible products analyzed by sexes after operation of filleting (Santos et al., 2026) and dehydration of the materials using an oven with previously established conditions (Figure 2) as for fish skin tissues (Rodrigues et al., 2025).

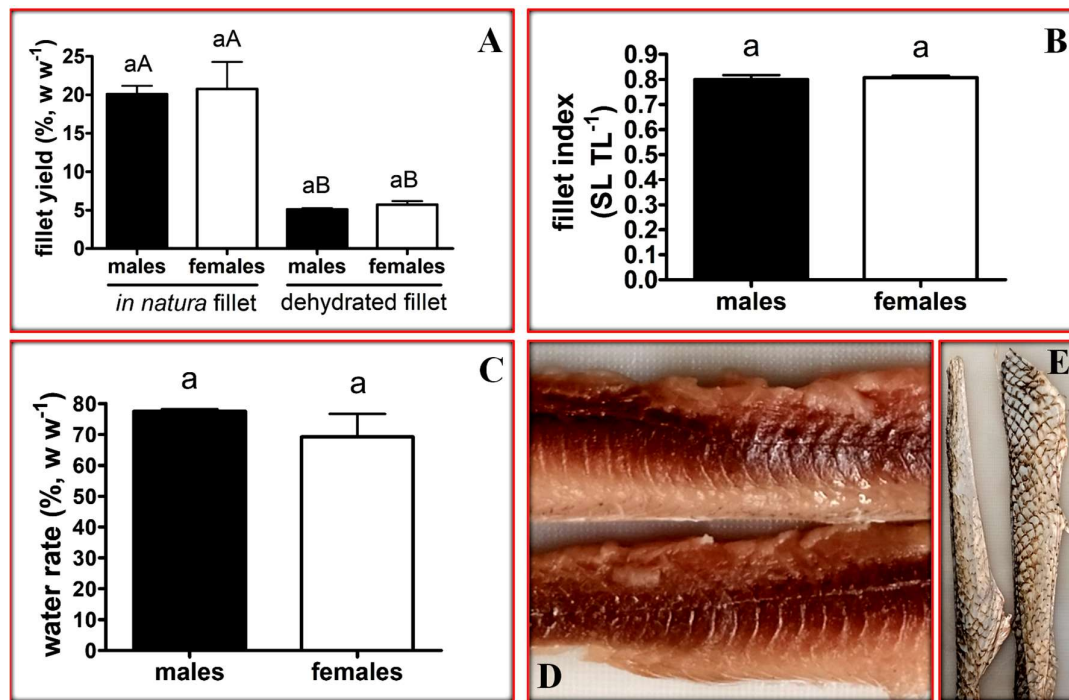


Figure 4. *In natura* or dehydrated fillet (A) yield, relative index of biometric composition (B) and water content (C) for captive *P. brevis* males and females. Skeletal muscle devoid of skin removed from the male body as an elongated edible product with central portion of red coloration (D); and skin tissue in the silvery colour of genus *Prochilodus* (E). Lowercase or uppercase letters on the bars indicate statistical significance between sexes or filltes (*in natura* and dehydrated), respectively, at level of 5 or 1% (Student' T-test, $p < 0.05$ or 0.01 , $n = 4$).

Fillets of *P. brevis* (a detritivorous fish) were estimated and compared for their *in natura* and dehydrated products between both sexes (Figure 4A). As expected on its quite homogeneous body standard in size and weight for both matured animals in captivity (Table 1), the edible masses showed a modest product ($22.69 \pm 1.24\%$, 38.05 ± 3.05 g - males vs. $20.75 \pm 3.51\%$ vs. 40.18 ± 4.36 g - females; $p >$

0.05) as previously analyzed ($21.15 \pm 5.10\%$, 28.31 ± 9.16 g - males vs. $18.84 \pm 6.52\%$, 37.62 ± 9.47 g - females) by Santos et al. (2026) speculating where the adaptability of the animals to a commercial feeding (Moreira et al., 2001; Salmito-Vanderley et al., 2023) conditioned and supplemented the species during the culture (Borba et al., 2026), as supported by the SL TL⁻¹ index (0.80 ± 0.01 - males vs 0.80 ± 0.00 - females, $p > 0.05$) (Figure 4B) (Santos et al., 2026). This is a point of view with relevance not only in biological terms (Baldiasserotto, 2002; Leite et al., 2018), but as also widely debated in the literature that a balanced feeding regulates the metabolism of fishes (Moreira et al., 2001), as well-evidenced herein without significant loss of edible mass and, consequently, with uniformity of the product from the animals (Moreira et al., 2001), even in its reproductive period (Figure 4A) (Santos et al., 2026). The captive stimuli could be suppressed by the lacking of hormonal functioning to spawning, achieved only in the laboratory (Leite et al., 2018; Vieira et al., 2024) aiming sustentability of *P. brevis* over time (Sales & Sales, 1990).

On the other hand, comparatively, these yields were less attractive than those of “traíra” *Hoplias malabaricus* fillets (48.635 - females vs. 46.12% - males by Santos et al. (2001) / 34.62 - 34.76% by Araújo et al. (2018)), of genus *Cichla* fillets (*C. monoculus* - 46.52 - 42.96% by Cosme et al. (2022) / *C. kelberi* - $38.13 \pm 5.41\%$ by Rodrigues et al. (2026)); and of genus *Prochilodus* fillets (*P. nigricans* - 32.52 - 29.54% by Souza and Inhamuns (2011) / *P. lineatus* - 42.70 - 41.06 by Borba et al. (2026)) when pre-processed/culture ou not, since several variables of anatomy and human operation affect the fish edible mass yield (Moreira et al., 2001).

Despite low amount, we also intended to determine the dehydrated mass (5.17 ± 0.21 - males vs 5.72 ± 0.46 - females, $p < 0.05$) (Figure 4A) as an additional subsidy on the intrinsic level of water present in captive *P. brevis* muscle (Figure 4C), in order to estimate any influence on its metabolic status inside the reproductive phase, applying the alternative method of Rodrigues et al. (2025) previously evaluating the biochemically stressed Nile tilapia (*Oreochromis niloticus*) under mesohaline conditions. In our case, both *in natura* muscles of captive *P. brevis* males and females were submitted to oven adjusted to $45\text{ }^{\circ}\text{C}$ for 24 h and the results revealed that the management adopted in captivity, as well as the stage of gonadal maturation observed in this study did not alter the species' hydric balance, even during this phase of reproduction. Although with a very small sample size (Table 1, Figure 4C), the average values of lost water in *P. brevis* muscle were from $69.19 \pm 7.49\%$ for females to $77.49 \pm 0.72\%$ for males; therefore, they were similar between both gender ($p > 0.05$), supporting the hypothesis that the species subjected to a controlled diet would produce a favorable physiological condition linked to reproduction, without compromising the body mass (Table 1) in line with Santos et al. (2026) and in biochemical processes developed by human techniques (Salmito-Vanderley et al., 2023; Leite et al., 2018; Vieira et al., 2024). It is important to note that there are little evidences on the water composition in fish tissues, varying with the species and somatic factors (Moreira et al., 2001; Ogawa & Maia, 1999) or, until,



when induced to saline stress (Rodrigues et al., 2025). The reproduction becomes the immunological system of the animals more exposed to sazonal variation (Baldissierotto, 2002) and diseases in aquaculture (Moreira et al., 2001).

As the determination of water revealed to be elevated (Figure 4C) because freshwater fish are hyperosmotics (Moreira et al., 2001) and edible parts are quite perishables to a rapid degradação by microbial agents (Ogawa & Maia, 1999), the controlled reduction in water of processed muscle was necessary to preserve the product's integrity against factors linked to post-mortem (Ogawa & Maia, 1999) for recovering, thereafter, of *P. brevis* muscle GAGs with greater security (Fernandes et al., 2025) to obtain they than in *in natura* (Rodrigues et al., 2025) comparing other studies (Hannesson et al., 2007; Jacobsen et al., 2019; Jridi et al., 2019; Wang et al., 2024; Cordeiro et al., 2026).

Intramuscular metachromatic sulfated GAGs yield

Crude GAGs yields from *P. brevis* skeletal muscle coincided with their metachromatic properties (Figure 5). On a mass-to-mass basis, the available amount differed ($p < 0.05$) between the sexes from $0.02 \pm 0.00\%$ (females) to $0.09 \pm 0.01\%$ (males) based on dehydrated first-matter ($w w^{-1}$) (Figure 5A), revealing metachromatic sulfated materials (Figure 5C-E) by the method of Farndale et al. (1976). In males, sequentially digested edible tissue also determined differences (0.07 ± 0.00 and $0.01 \pm 0.00\%$ for M1-GAGs and M2-GAGs, respectively, $p < 0.05$ - Figure 5A) in the distribution of GAGs in same animal muscle similar to seaweed cell-wall polysaccharides, although evolutionarily distant (Pomin & Mourão, 2008). Despite the similarities in anatomy and body yield (Table 1, Figures 4) (Santos et al., 2026), *P. brevis* of both sexes could differ among them in the complexity of the extracellular matrix to access GAGs comparing other sources (Tingbo et al., 2005; Hannesson et al., 2007; Jridi et al., 2019; Cordeiro et al., 2026), perhaps as an indirect result of the reproducible cycle of the species of total spawning (Gurgel et al., 2012; Nascimento et al., 2012; Bomfim et al., 2015). For sea urchin (*Lytechinus variegatus*), the temperature influence on the expression of polysaccharides by invertebrate (Pomin & Mourão, 2008). GAGs prospects is in line with the increased global demands for exploring of various animal sources (Badri et al., 2018; Balbinot-Alfaro et al., 2021) since animal body-connected parts (Hannesson et al., 2007; Wang et al., 2024; Fernandes et al., 2025) to related factors (Rodrigues et al., 2025).



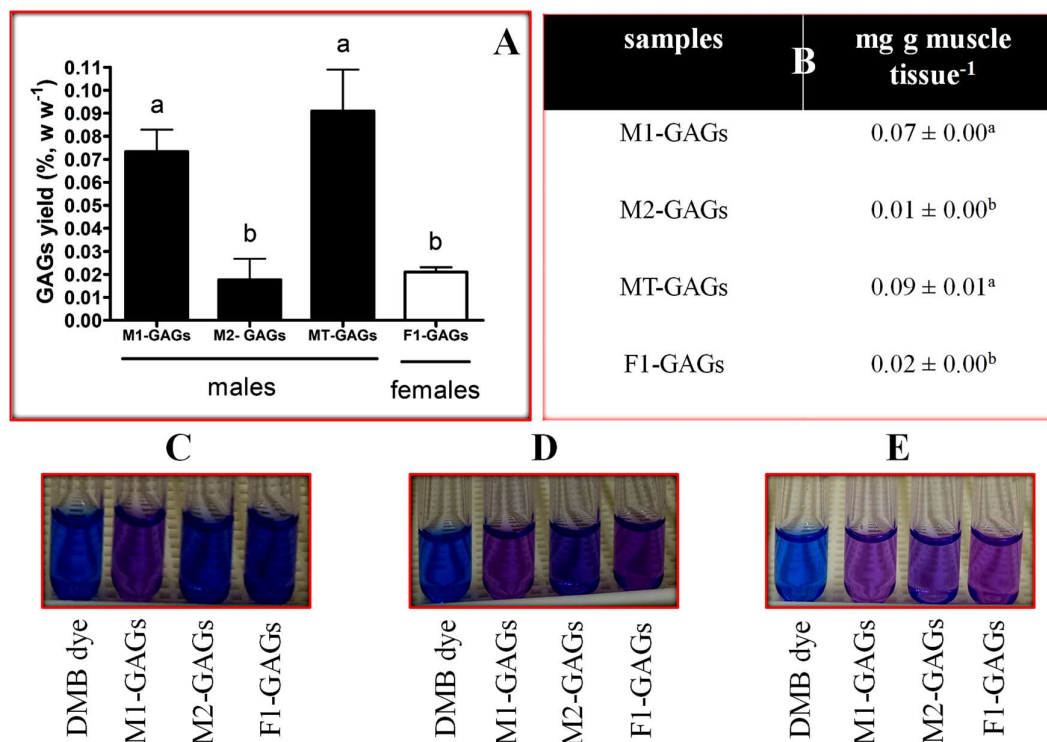


Figure 5. Extraction yield (% w w⁻¹, or mg per gram (g) of muscle tissue - A, B) and metachromasy with the DMB dye (9 - C, 18 - D or 27 µg - E) of crude GAGs from captive *P. brevis* (males and females) muscles. Different letters indicate statistical significance at level of 5 or 1% (ANOVA, Tukey' test, $p < 0.05$ or 0.01 , $n = 3$).

Structure of muscle tissue varies with the species (vertebrates / invertebrates), not only in type (striated or smooth), but also in fibers (myotome), which are connected by membranes called myomata and, until, collagen, resulting in sarcolemma membrane that covers the muscle fibers (Ogawa & Maia, 1999). In vertebrate phylum, the content of GAGs in the intramuscular connective tissue is also dependent of the somatic factor involved in the animal body. A study performed by Hannesson et al. (2007) revealed that differences in the skeletal muscle' architecture between the fish cod (*G. morhua*) wild caught maintained in cage-type captivity and the young bulls (Norwegian red) resulted at a significant level of GAGs for the bovine muscle ($510 \pm 42 \mu\text{g GAGs g wet weight}^{-1}$) than that in fish one ($325 \pm 58 \mu\text{g GAGs g wet weight}^{-1}$). For the cuttlefish muscle (*Sepia officinalis*), Jridi et al. (2019) obtained 8.6% average extraction amount for GAGs (w w⁻¹). Recently, juveniles *Litopenaeus vannamei* (an invertebrate) crude GAGs from muscle samples yielded about $0.7 \pm 0.03 \text{ mg GAGs g dehydrated weight}^{-1}$, when they cultured in mesohaline water (Cordeiro et al., 2026), therefore, a recovered mass, at least, 10-fold higher than our study. These combined scenarios suggested that the extracellular matrices of the connective tissue in these aquatic sources were more abundant in GAGs than in matured *P. brevis* muscle (Figure 5A, B).

Apparently, sulfated GAGs composition seems be different in captive *P. brevis* muscle between both gender as metachromically evaluated by the method of Farndale et al. (1976) from the analyzed polymer samples (Figures C, D, E). It

seemed that the relative degree of indirect detection with the DMB dye for the matured males muscle-derived GAGs was to be a more specific cationic dye-binding capacity than observed for females one, which required 3-fold higher of sample for to reaching the violet reaction to that of males (Figure 5E). Results suggested that the cycle of *P. brevis* also depends the sulfate content of GAGs stored in the muscle tissue, being this biological demand more targeted at females, which produce vitellogenesis (Baldisserotto, 2002) utilizing the available muscle energy as in other fish species (Moreira et al., 2001; Santos et al., 2001; Araújo et al., 2018). Although no difference in relative fillet mass (Figure 4A), possibly as a result of the commercial feeding (Moreira et al., 2001), the distinct electrostatic environment in reproductive phase changed between the matrix of the skeletal muscle of *P. brevis* males and females unrelated to its water rate (Figure 4C), but within for teleost fish (60-85% water) (Ogawa & Maia, 1999).

Sulfate composition in GAGs varies among species (Pfeiler, 1998; Tingbo et al., 2005; Jacobsen et al., 2019; Jridi et al., 2019; Wang et al., 2024; Cordeiro et al., 2026) and in adverse conditions (Pomin & Mourão, 2008; Fernandes et al., 2025; Rodrigues et al., 2025). The dark striated (red muscle) organization of muscle fiber along the central axis of the fish fillet was consistent (Figure 4D) (Ogawa & Maia, 1999) and could have a higher concentration of water, lipid and proteins (Sales & Sales, 1990) common for migratory fish (Ogawa & Maia, 1999). Consequently, intramuscular GAGs composition may reflect the environmental challenges (Hannesson et al., 2007), especially in muscle biomechanical related to contraction and architecture (Ogawa & Maia, 1999), since the *P. brevis* fish has a migratory behaviour (Gurgel et al., 2012; Nascimento et al., 2012), but it could be different in captivity (Moreira et al., 2001). GAGs in muscle tissue of spotted wolffish, *Anarhichas minor* (a non-gaping species) and Atlantic cod, *Gadus morhua* (a gaping species) differed not only in terms of sulfate anionic composition between both fish species, but also in type of matrix' GAG (Tingbo et al., 2005). For GAGs extracted from bovine (Norwegian red) and from Atlantic cod (*G. morhua*) skeletal muscle, Hannesson et al. (2007) speculated functional requirements associated with the fibrous appearance and texture of muscle. Diversities of GAGs were already reported for cuttlefish (*Sepia officinalis* - Jridi et al., 2019), salmon (*Salmo salar* - Jacobsen et al., 2019), flounder (Wang et al., 2024) and shrimp (*Litopenaeus vannamei* - Cordeiro et al., 2026) regarding bioactivities and/or muscle-related biochemical factors, as gaping of fillets (Jacobsen et al., 2019).

Of particular importance was to aligns the findings regarding the stage of the gonadal maturation and intramuscular GAGs composition. So, as artificial dietary supplementation prevented the loss of edible mass and water (Figure 4), the stage of gonadal maturation significantly influenced on the sulfated GAGs level in captive *P. brevis* muscle (Figure 5). This profile, however, was yet distinct from the GSI (Table 2), which it showed inversely values to intramuscular GAGs concentration, possibly *P. brevis* direct their bodily energy also toward in semen production (Leite et al., 2018; Vieira et al., 2024), since Nile tilapia skin GAGs-cryopreserved *P. brevis*



semen were demonstrated *in vitro* (Nascimento et al., 2021), except for those *in vivo* studies yet not performed by our group. On the other hand, compromise of the muscle matrix could affect meat quality and the animals vulnerable to diseases, given the reproduction decline immune defences against microbial pathogens (Moreira et al., 2001).

On a structural basis, GAGs from *P. brevis* (males and females) muscles were, thereafter, analyzed by FT-IR spectroscopy to identify any molecular variation.

Structural composition of *P. brevis* muscle GAGs by FT-IR analysis

Structure analysis of the *P. brevis* GAGs from dehydrated muscle samples was conducted and compared for both sexes using FT-IR spectroscopy (Figure 6). Some variations of chemical signals were noted among the samples (M1-GAGs vs. M2-GAGs and F1-GAGs), especially for total sulfation and position of sulfate in their respective polysaccharidic chains, but they were overall compatible with the anionic character as already mentioned by metachromasy analysis (Figure 5C, D, E). Additionally, all the spectra were to be similar to those of the cuttlefish (*S. officinalis* - Jridi et al. (2019)) and shrimp (*L. vannamei* - Cordeiro et al., 2026)) muscle GAGs, respectively, which inconclusive regions were yet observed, possibly the high level of contaminants present in *P. brevis* muscle (Cordeiro et al., 2026) due to high values of protein (Sales & Sales (1990) could mask the polysaccharidic samples, since the edible mass has an extracellular matrix constituted in muscle fibers also organized by proteoglycan-structures constructed by complex GAGs chains connected to a protein core (Badri et al., 2018; Balbinot-Alfaro et al., 2021; Ricard-Blum et al., 2024).

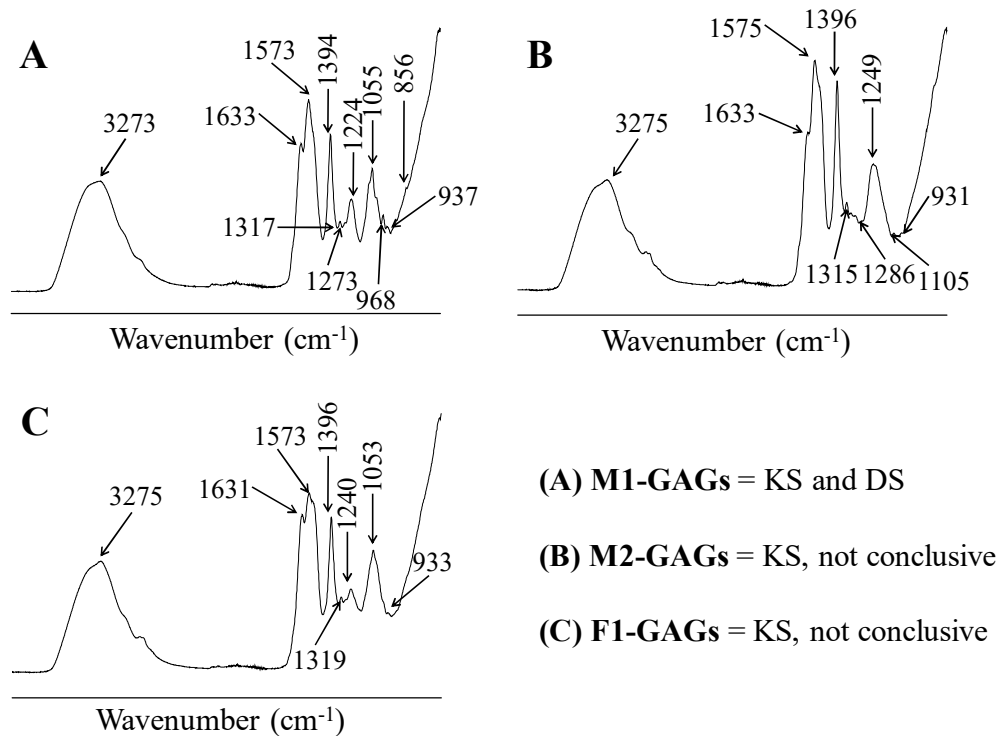


Figure 6. FT-IR spectra of the *P. brevis* GAGs from muscle samples (M1-GAGs: A, M2-GAGs: B, and F1-GAGs: C) obtained from kBr pellet at 500 4000 cm^{-1} .



Despite some unresolved signals, typical structures for papain-extracted polysaccharides from *P. brevis* dehydrated muscle were identified as those three characteristic bands of amides (3273-3275 - amide I, 1631-1633 - amide II and 1573-1575 cm^{-1} - amide III) with intensity similarities (Jridi et al., 2019; Fernandes et al., 2025; Rodrigues et al., 2025; Cordeiro et al., 2026). As also indicated from the spectra, all the samples contained uronic acids ($\text{O}=\text{C}=\text{O}$: 1394-1396 cm^{-1} , except for bands around 1400 cm^{-1} commonly observed in other aquatic sources (Jridi et al., 2019; Fernandes et al., 2025; Rodrigues et al., 2025; Cordeiro et al., 2026), carboxylated groups making part of the residual acid sugars (Badri et al., 2018; Balbinot-Alfaro et al., 2021; Ricard-Blum et al., 2024). As expected, HA structures was also not found in examined samples (Tingbo et al., 2005; Hanneson et al., 2007; Jridi et al., 2019), a pharmaceutically important-unsulfated GAG (formed by uronic acid and hexosamine) possessing a molecular mass more than 100 KDa (Fernandes et al., 2025), frequently occurring in skin and cartilage, for skin repair and wound healing properties (Badri et al., 2018; Balbinot-Alfaro et al., 2021; Ricard-Blum et al., 2024). More recently, Wang et al. (2024) detected HA in several tissues (bone, muscle, skin and viscera) of flounders.

More intriguing was to the sulfate-related intensity and the occurrence of polysacchadic classes in same or between both sexes (Figure 6) (Jridi et al., 2019; Fernandes et al., 2025; Rodrigues et al., 2025) by accessing crude GAGs (M1-GAGs, M2-GAGs and F1-GAGs) by sequential tissue digestions (Figure 3) selectively in yield from the same fillet properties (Figures 5A, 4). There were similarities among the spectra (Figure 6), but the structural composition between M1-GAGs vs. M2-GAGs and F1-GAGs was more relevant, since both signals at 856 (C-O-S) and at 931-937 (3,6 anhydrogalactose) cm^{-1} (DS and KS, respectively) (Fernandes et al., 2025; Rodrigues et al., 2025) were attributed to M1-GAGs (first extraction), while for M2-GAGs (redigestion) and F1-GAGs (first extraction) at 856 cm^{-1} was not revealed (Figures 6B, C).

Bands related to acetylated galactosamine residues for acetyl groups ($\text{C}=\text{O}$, at 1573-1575 cm^{-1}) were still pointed for all the analyzed polymer samples (Figure 6). They also confirmed for DS structures in male *P. brevis* muscle and, possibly, they were produced by the sampled females fillets, since the skin and bone are attached to fillet (Figure 4D) and biochemical connections would occur anatomically by their related fluids (Moreira et al., 2001; Wang et al., 2024). In fact, as DS was found in a considerable level in *P. brevis* skin in another study (Fernandes et al., 2025), this hypothesis was not discarded, even in the absence of specific sulfation (Figure 6C). In Nile tilapia, DS was implied as a modulator inside the ionic balance with water loss by fish skin, when in mesohaline conditions (Rodrigues et al., 2025).

In this study, both DS and KS GAGs could be concerning functional roles in red striated muscle, as in fibrous appearance and texture of tissue (Figure 4D) (Hannesson et al. (2007) varying their concentration and negative charge density (Pfeiler, 1998) between the sexes inside the gonadal development (maturation) (Figure 5) (Zhang et al., 2009). Such issues were more drastics in females (Figure 5)



as supported by FT-IR spectrum showing more reduced absorption bands (Figure 6C) suggesting any energetic use by fish (Moreira et al., 2001; Baldisserotto, 2002), although without loss of fillet mass (Figure 4), compensated by artificial feeding (Santos et al., 2026). DS is a hybrid structure from CS ones that interacts with the collagen fibrils, favouring cell proliferation and differentiation. Even KS contains galactose and sulfate group also occupying at the carbon 6 of the polysaccharide chain with role related to development and regeneration, but it has not yet been completely studied in various systems (Balbinot-Alfaro et al., 2021). In the male GAGs spectrum, both polymers were apparently coextracted (M1-GAGs) by papain method (Figure 6A), suggesting that the powdered muscle tissue generated a contact area for enzymatic action and it helped in its efficiently identification of the animal site (Figure 3). Gaping-related factors have also been attributed to the level of sulfated GAGs and type in the fish muscle (Tingbo et al., 2005).

Degradation of proteoglycans-structures is industrially achieved (Badri et al., 2018; Balbinot-Alfaro et al., 2021), but it aligned to texture and muscle cohesion (like gaping) has been little understood (Ogawa & Maia, 1999; Jacobsen et al., 2019). The wide diversity of species and their various reproductive strategies (Moreira et al., 2001) condition the physiological responses to climatic factors (Baldisserotto, 2002) challenging the study of the biological mechanisms involved in reproduction (Leite et al., 2018; Nascimento et al., 2021) for migratory fishes (Baldisserotto, 2002; Soares et al., 2021). Current investigation brings, for the first time, a biochemical approach aligned to comparative biology of captive common curimatã (*P. brevis*) for examining both sexes. The study governed new perspectives on the use of edible mass of *P. brevis* fish as a site to explore the participating of GAGs as biomarkers related to physiological status and standard of fresh appearance attributed to availability and structural composition inside the reproductive phase. *P. brevis* could be a model organism for investigating of its sexually matured specimens presenting the total spawning as reproductive strategy. A more detailed study regarding the overall ontogenetic development on this theme is still in progress.

Conclusion

The stage of gonadal maturation did not cause any change in the edible mass of *Prochilodus brevis* in captivity. The profile of intramuscular glycosaminoglycans, however, showed at level of yield and structural composition, with significantly important differences in the skeletal muscle between both gender for the anatomically homogeneous standard in weight and size evaluated. The presence or not of dermatan and keratan structures was partially characterized by sequentially papain-assisted technique followed by infrared spectroscopy, governing their access and identification in the extracellular matrix of the connective tissue and, in parallel, the physiological balance was maintained hydrating the tissue and the metabolism favorable to reproduction. Findings pointed out the glycosaminoglycans in striated muscle site as bioenergetic markers connected inside the reproductive cycle, but with demands inversely to the gonadosomatic index determined by the sexual maturity of the species with total spawning.



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